Impact of foot-and-mouth-disease on goat behaviour after experimental infection with serotype SAT1 virus

Tanja E. Wolf[1], David D. Lazarus[2,3], Pamela Opperman[2,4], Livio Heath[4], Andre Ganswindt[1], Geoffrey T. Fosgate[2]

[1] University of Pretoria, Mammal Research Institute, Pretoria, South Africa

[2] University of Pretoria, Faculty of Veterinary Science, Department of Production Animal Studies, Onderstepoort, South Africa

[3] National Veterinary Research Institute, Foot-and-Mouth Disease Virus Laboratory, Vom Nigeria

[4] Agricultural Research Council, Onderstepoort Veterinary Research, Transboundary Animal Diseases, Onderstepoort, South Africa

Abstract:

Infectious diseases and parasitic infestations can cause a set of non-specific clinical signs, such as increased body temperature and resting, and a decrease in food intake. These physiological and behavioural changes have an adaptive function facilitating defences against the pathogen and to support immune functions. These so-called 'sickness behaviours' can also be used as an early detection tool for disease. Foot-and-mouth disease (FMD) still causes great economic losses in endemic countries, especially to smallholder farmers. The aim of this study was to determine if behavioural changes in goats can be used as an early indicator of FMD virus (FMDV) infection. The efficacy of a Southern African Territories (SAT) FMD vaccine was studied on forty South African indigenous goats. Changes in daily activities (resting, feeding, walking), as well as social behaviours (social resting, social feeding, dominance behaviours) were recorded and then compared over time and between clinically affected and unaffected goats. Pedometers were used to estimate average daily steps and to compare between groups of study animals.

Eleven goats developed clinical signs of FMD, as well as non-FMD related sicknesses during the course of the study. Overall walking and resting behaviours were not significantly affected by the presence of FMD related clinical signs ($p > 0.05$). However, during the time of FMDV infection, social resting increased significantly ($p < 0.001$). Although goats developed FMD lesions on lips and tongues, percentage of time feeding was not affected ($p = 0.762$), suggesting that the study goats did not perceive the oral lesions as an important disturbance. Similarly, the number of steps did not consistently decrease in the presence of FMD-associated foot lesions. When affected by non-FMD related sicknesses, animals did not have an overall reduction in the time spent feeding ($p = 0.867$). However, goats affected with non-FMD conditions reduced the amount of social feeding ($p = 0.002$), potentially avoiding energetically costly competition at the feeding points. Overall, goats affected with FMD did not show more sickness behaviour, suggesting that FMDV infection in goats might not lead to obvious and therefore, easily detectable behavioural changes. This might have implications for farmers and animal health personnel, as individual goats infected with FMDV might be

undetected within a flock due to the absence of obvious sickness behaviours, and the virus can therefore be spread more easily between herds through animal movements.

Keywords: Activity budget, Dominance, Sickness behaviour, South Africa, Surveillance

1. Introduction:

Infectious diseases and parasitic infestations can cause a set of non-specific clinical signs that include increases in body temperature, loss of interest in common daily activities, decrease in food intake, and occurrence of lethargy (Dantzer et al., 1996; Hart, 1988). Traditionally these signs, and specifically the behavioural changes mentioned, have been classified as the inability of the animal to accomplish their normal activities due to the debilitation caused by the disease (Aubert, 1999). More recently, these changes have been interpreted as adaptive functions to facilitate defences against the pathogen by conserving energy that could be used to support the immune response. Rather than being maladaptive, these so-called 'sickness behaviours' are behavioural strategies that serve as a first line of defence before the immunologic response is activated and might be critical to the survival of an individual (Hart, 1988). The behavioural changes linked with sickness centre around a fever response, a higher body temperature stimulates the immune response and is also unfavourable for the survival of many bacterial and viral pathogens (Kluger, 1986). However, increasing the body temperature is energetically costly, and therefore a reduction in activity and an increase in resting are considered a strategy to conserve energy in order to raise body temperature. In addition, animals often curl up or adopt a hunched position to insulate themselves (Aubert, 1999; Hart, 1988). Beside an increase in resting behaviour, anorexia might also have a positive effect on the recovery of sick animals. In mice for example, a positive relationship was found between weight loss and survival when infected with *Listeria monocytogenes* (Murray and Murray, 1979). Additionally, for wild animals foraging or hunting can expend energy that is needed to maintain a fever response or make weakened individuals an easy target for predators (Johnson, 2002).

Diseased rats, for example, shift their behavioural priorities in a manner that benefits recovery (Lopes, 2014; Miller, 1964). When challenged with endotoxins, rats tended to remain at rest rather than move to receive a reward. Animals are still reactive to their environment when expressing sickness behaviours, and these behaviours have therefore been characterised as a motivational state (Miller, 1964). A variety of biotic and abiotic factors, including season and sex can affect the expression of sickness behaviours (Avitsur and Yirmiza, 1999; Lopes, 2014; Owen-Ashley et al., 2006; Owen-Ashley and Wingfield, 2006). Further, the social environment can also have an effect on the expression of sickness behaviours; the costs and benefits associated with survival and for example reproductive success should be considered (Lopes, 2014). Living in groups comes with certain costs, one of them being a potential increase of disease transmission. An increase in group size is positively associated with parasite and pathogen prevalence (e.g. Chapman et al., 2009; Godfrey et al., 2006). Studies of house finches (*Carpodacus mexicanus*) and Toque macaques (*Macaca sinica*) have shown that healthy individuals can change their behaviour in the presence of sick or injured group members (Bouwman and Hawley, 2010; Dittus and Ratnayeke, 1989). Additionally, higher ranked individuals can afford to engage in sickness behaviours, while subordinates might be motivated to conceal their sickness in order to maintain their rank (Cohn and de Sá-Rocha, 2006; Fairbanks and Hawley, 2012; Lopes, 2014).

From an animal management point of view, changes in daily behaviours can be a useful indicator for veterinarians to assess the health of farm animals (Broom, 1987). For example, feeding, as well as gait changes occur in cows that are affected with acute mastitis (Siivonen et al., 2011). However, an animal's behavioural responses can vary depending on its individual pain threshold, as well as on the disease and how severely it affects the physiological functioning (Kemp et al., 2008; Siivonen et al., 2011). An early detection of sickness within a herd can help reduce pathogen spread and therefore prevent larger losses of animals and reduce treatment costs. This is of special importance in smallholder farmers.

Foot-and-mouth disease (FMD) is caused by a RNA virus (FMDV), belonging to the genus *Aphthovirus* within the family *Picornaviridae.* Seven serotypes of FMDV have been described, with the Southern African Territories (SAT) 1 to 3 originating from southern Africa (Jamal and Belsham, 2013). Clinical signs of disease include increased body temperature, excessive salivation and the formation of lesions on the oral mucosa and the inter-digital spaces of the feet (Jamal and Belsham, 2013). There is a paucity of literature concerning FMD in goats. However, in experimentally infected goats, clinical signs have been described as mild with a rise in body temperature, nasal discharge, and ulcerative lesions of the oral mucosa and feet (Lazarus et al., 2019). Although eradicated in many developed countries, FMD still causes great economic losses in endemic countries, especially to smallholder farmers (Nampanya et al., 2015). During 2019, outbreaks of FMD were reported in cattle within the previously FMD-free zone of South Africa (DAFF, 2019). Goats have also been suggested to be involved in previous FMD outbreaks in southern Africa (Lazarus et al. 2019). In South Africa goats are the most common livestock species of communal or smallholder farmers, and small ruminant flocks are often unsupervised employing free-roaming grazing during the day (Mohlatlole et al., 2015) while often housed or kraaled together with cattle during the night. The aim of this study was to determine if experimental infection with SAT1 FMDV induces detectable behavioural changes in goats in an attempt to improve surveillance efforts in endemic countries with large domestic goat populations.

2. Material and Methods:

2.1. Study animals

Forty FMD-free indigenous South African goats 6-8 months of age including both sexes were obtained for the evaluation of a newly developed FMD vaccine (Lazarus et al., submitted). The evaluated vaccine was a high potency oil emulsion that contained two SAT1, two SAT2 and one SAT3

FMDV. The forty goats were randomised into five treatment groups including two control groups of five animals each: one group received a full cattle dose and the other an adjuvant-only placebo. Three additional groups were treated with reduced doses (1/3rd, 1/16th, 1/12th) of the vaccine. All treatments were administered into the left prescapular musculature.

Goats were stratified by source and sex and randomly assigned to one of the five vaccination treatment groups. Each group was housed in a separate biocontainment room (stable) within a biosafety level 3 animal facility at the Transboundary Animal Diseases platform within the Onderstepoort Veterinary Research (OVR) campus of the Agricultural Research Council. Goats were experimentally challenged by intra-dermolingual inoculation on the dorsal surface of the tongue using a pool of three SAT1 (SAR/8/10, SAR/10/10 and SAR/21/10) serotype FMDV (Lazarus et al., 2019).

The animals were fed a complete pelleted ration once a day and had access to fresh water *ad libitum*. Animal use protocols were reviewed and approved by the OVR (AEC 6.17) and the University of Pretoria (AEC V022-17).

2.2 Data collection

Behavioural data were collected using scan sampling for daily activities and continuous sampling for social behaviours (Martin and Bateson, 2007). The complete trial period was divided into three phases: Phase 1: Time between first and second FMD vaccination (20 d), Phase 2: from second vaccination until FMDV experimental challenge (21 d), and Phase 3: post-challenge (14 d). Each treatment group was observed twice a week over a 1-hour observation period during Phase 1 and 2. During Phase 3, each group was observed for 30 minutes each day. The order of observations was varied to prevent data collection from having a cyclical pattern; however, the sequence of group observations could not be formally randomised because of the routine animal procedures implemented as part of the FMD vaccination study.

Prior to the start of Phase 3, pedometers (Volkano Fit Series) were fitted above the left tibiotarsal joint of each goat using Velcro straps and elastic bandage material. The numbers of steps were recorded on a daily basis in the mornings during the clinical examinations performed as part of the vaccine efficacy study.

Daily activity budgets were determined using scan sampling at five-minute intervals. The following behaviours were recorded: Resting (both solitary and social standing, drowsing, laying, laying and drowsing, sleeping), feeding (both solitary and social feeding, drinking), ruminating (both solitary and social ruminating in standing or laying position), locomotion, dominance behaviour (dominating other individuals by gesture or physical contact, yielding from other individuals, displacing others or being displaced), and play behaviour (both solitary or social) (Da Silva et al., 2013). Due to their rare occurrence, the following behaviours were summarised together as 'Other behaviours': following another individual, urinating / defecating, investigating other individuals, and interaction with humans. Daily activity budgets were calculated as percentages of scans in which the specific behaviour was recorded (percentage of time).

Social behaviour was recorded continuously during each observation period. The following behaviours were recorded: Contact behaviour (rubbing, grooming, sniffing), feeding, play, resting (both in standing and laying position), sexual behaviour (following, mounting, investigating, urine testing), dominance behaviour (physical aggression, dominance gestures, displacing), and submissive behaviour (yielding, being displaced) (Da Silva et al., 2013). Changes in dominance behaviour over time was further investigated by focussing on physical aggression and dominance gestures, displacing other individuals, yielding, and being displaced by other individuals.

2.3 Statistical analysis

The health of an individual goat was categorised within each time phase as having shown signs of FMD, signs of another disease or injury, or no disease or injury present at any time during the phase.

Fever was defined as a body temperature ≥40°C. Daily activities (walking, feeding, resting) were analysed as percentages whereas occurrence of social behaviours (social resting, social feeding, dominance behaviours) were analysed as counts per hour. All behaviours were summarised by phase creating one data point per individual per phase. Data were evaluated for normality and subsequently social resting and feeding rates were natural logarithm transformed, while all dominance behaviours were rank transformed prior to statistical analysis. Due to logistical constraints, the observation time during Phase 3 was changed to 30 mins per day in order to observe all individuals on a daily basis (when changes in behaviour due to FMDV infection would occur). Mixed-effects linear models with the specific behaviours as the response variables were fit using the function lmer of the R-package lme4 (Bates et al., 2013). Phase, sex, weight, non-FMD sicknesses and FMD lesion presence were evaluated as fixed effects (Mundry, 2014). Animal ID and stable (treatment group) were included as random effects to account for the repeated measures design and group effects related to housing and vaccine dose. The inclusion of both random effects sometimes caused overfitting (singular fit model) and when this occurred one of the random effects was excluded. Fixed effects that were not significant were subsequently excluded from the final models (Schielzeth, 2010).

Similar mixed-effects models were fit to analyse daily pedometer data. The steps were analysed using daily values, with data being natural logarithm transformed to improve the distributional form prior to statistical analysis.

All statistical analyses were performed using the program R, version 3.5.2 (R Core Team, 2013) and significance was set as $P < 0.05$.

3. Results:

3.1 Descriptive results

Three animals died from non-FMD related causes during Phases 1 and 2 and were subsequently omitted from the analysis.

Each of the five treatment groups was observed for a total of 22 hours over the course of the study period (Phase 1: 6 hrs, Phase 2: 6 hrs, Phase 3: 10 hrs). During this time, a total of 7548 daily activities were recorded (Phase 1: 2664, Phase 2: 2664, Phase 3:2220). Over the entire study period, 4983 social behaviour events were recorded (Phase 1: 1628, Phase 2: 1751, Phase 3: 1604).

Some goats were diagnosed with non-FMD sicknesses including infectious keratoconjunctivitis and respiratory disease, presumably due to the intermixing of study animals from multiple sources. In total, 11 individuals were affected with a non-FMD sickness (Phase 1: 7, Phase 2: 4, Phase 3: 0) and 11 individuals developed FMD-specific secondary lesions during Phase 3 (primary lesions at the site of challenge were not considered).

Some of the observed behaviours (play, contact and sexual behaviour) were omitted from analysis due to their rare occurrence and infrequent detections.

3.2 Daily activity / scan sampling

Walking behaviour was recorded on average 7% of the time (absolute range 0 – 19%, see table 1). Resting behaviour (social and solitary) occurred on average in 50% of the recordings (range 13 – 80%), comprising of resting while standing (19%, range 2 – 95%) and laying down (31%, range 0 – 70%). During 23% of the time, the animals were feeding. There was no significant difference across study phases for any of these behaviours. However, females spent significantly more time resting compared to males ($p = 0.007$, see table2). No significant differences occurred in any of the daily activities in goats affected with secondary FMD lesions (Supplemental table 1).

3.3 Social behaviour / continuous sampling

Social feeding occurred on average twice per hour (range 0 – 6, see table 3) over the three study phases. FMD clinical signs were not significantly associated with changes in social feeding and were subsequently removed from the final models (Supplemental table 2). Social feeding was significantly higher in Phase 3 compared to the beginning of the study period (Phase 1, p = 0.025, see table 4). Non-FMD sickness had a significant effect on the social feeding, with less social feeding occurring when animals displayed signs of sickness (p = 0.033).

Social resting occurred on average 3 times per hour (range 0 – 8) during the three study phases. This behaviour was significantly different between the phases, with a higher occurrence during Phase 3 compared to Phase 1 (p < 0.001, see table 4). Non-FMD sickness had a significant effect on social resting with a decrease being observed during the times when animals showed signs of sickness (p = 0.002). The weight of animals also affected the social resting behaviour with increasing weight of an individual being associated with more social resting behaviour (p = 0.019, see table 4).

3.4 Dominance

FMD clinical signs were not significantly associated with changes in dominance behaviours and were subsequently removed from the final model (Supplemental table 2). During Phase 2, a significant decrease in agonistic behaviour was recorded compared to Phase 1 (p = 0.006, see table 5). This behaviour increased again in Phase 3 and although still less than Phase 1, this difference was no longer significant. Agonistic behaviour decreased significantly when the animals showed signs of respiratory disease (p = 0.013) and increased with the weight of the individual (p < 0.001).

More displacing behaviour took place during Phase 1 compared to Phase 2 (p = 0.004) and Phase 3 (p = 0.003), with heavier individuals performing more displacing behaviours (p = 0.006). The likelihood of being displaced was not significantly affected either by the Phase, or by any of the observed sicknesses. Yielding behaviour was increased during Phase 3 compared to Phase 1 (p = 0.029). When showing signs of non-FMD sickness, individuals displayed less yielding behaviour compared to when they were healthy. Males were less likely to yield than females (p = 0.005).

3.5 Daily steps

During Phase 3, the average number of steps per individual was 5380 per day (range 560 – 12931, see figure 1). The number of steps (natural logarithm transformed) were affected by the sex of the animals, with females walking more steps than males (regression coefficient: 0.51; 95% CI 0.05, 0.96; p=0.036). The number of steps was not significantly affected by whether or not FMD foot lesions were present (regression coefficient: -0.36; 95% CI -0.83, 0.17; p = 0.191), although two individuals had a decrease in steps when lesions were present (see figure 2). Goats took fewer steps per day when fever was present (regression coefficient: -0.33; 95% CI -0.11, -0.61; p = 0.006).

4. Discussion

Goats are the most common livestock species of communal, smallholder farmers in South Africa and an early detection of sicknesses within a herd might reduce production losses and reduce overall treatment costs. Additionally, outbreaks of FMD outside the protection zone has a large effect on the commercial sector due to loss of international markets and therefore affects the meat industry of the whole country. FMD is characterised by fever and lameness due to ulcerative foot lesions (Arzt et al., 2011) and clinical signs in goats have been described as mild with nasal discharge, ulcerative lesions of the oral mucosa and the development of fever (Lazarus et al., 2019). However, reports of FMD in goats are based on clinical signs extrapolated from what has been observed in sheep with very few goat-specific peer-reviewed publications. In our study, we evaluated the effects of an experimental SAT1 FMDV infection on the behavioural inventory of goats and the usefulness of these potential behavioural changes as a diagnostic tool for FMD surveillance. The clinical signs observed in this study were consistent with the clinical signs that are expected to occur in small ruminants (Kitching and Hughes, 2002).

Anorexia is a sign of sickness in many animals (Hart, 1988). Under natural conditions, foraging can take up a considerable amount of energy that might be needed to facilitate a fever response, additionally it places weak individuals under the risk of predation (Johnson, 2002). It has also been shown that reduced food intake and weight loss has a positive effect on the survival of diseased mice (Murray and Murray, 1979). During the current study, there were no changes in the amount of time spent feeding during the different phases but this might be due to the study methodology, as the frequency of food intake was recorded and not the quantity. It is therefore possible that FMDV infected individuals reduced the total amount of food that was consumed. However, the animals continued to gain weight during all phases of the study (Lazarus et al., 2019) and it can therefore be assumed that no changes in food intake occurred. Similarly in a study of red colobus monkeys (*Procolobus rufomitratus*), no significant effect on the feeding frequency was detected when individuals were infected with whipworms (Ghai et al., 2015). However, those authors did find a change in the composition of consumed food. In the present study, goats were fed commercial pellets and potential changes in feeding preference could not be investigated. Thus, further observations of sick goats would be necessary to investigate changes in food choices as a potential indicator of sickness. Yet, differences in social feeding were recorded, with the lowest occurrence of social feeding when animals showed signs of non-FMD sickness during Phase 2. A possible explanation could be that although the animals did not reduce their overall feeding frequency, they increased the amount of solitary feeding compared to feeding with other individuals, potentially avoiding energetically costly competition at the feeding points. Interestingly, the highest frequency of social feeding occurred during Phase 3 after individuals had been infected with FMDV. Although FMD affected animals developed oral lesions on their tongues and lips (Lazarus et al., 2019), they did not reduce their daily food intake. This might indicate that these lesions were not a painful disturbance. These findings suggest that FMD does not cause a change in feeding behaviour and is therefore not a reliable indicator for an early detection of FMDV infections in goats.

Sick animals are often described as being less active and more sleepy (Hart, 1988). Less movement and a curled up position can help conserve energy for a fever response and is complementary with anorexia to help the animal remain in heat preservation mode (Hart, 1988). The goats in this study affected by non-FMD related sicknesses were often observed in a hunched posture, presumably to conserve body heat. Resting behaviour in the goats of this study was affected by different factors. Females displayed more resting behaviour than males. A possible explanation could be that males are more often involved in other activities including searching for receptive females or defending a territory / maintaining social hierarchy. These activities can lead to an increase in movement and social activities and therefore cause less feeding or resting activities (Clutton-Brock et al., 1988). In this study, a higher body weight was also associated with a higher frequency of resting. This is similar to what has been observed in dairy heifers, where more lying periods are correlated with a higher daily weight gain (Mogensen et al., 1997).

Less social resting occurred when animals had signs of non-FMD sickness. Although some social behaviours are relevant for the individual fitness, social interactions can also create an opportunity for disease transmission (Lopes, 2014). It might be beneficial for healthy individuals to avoid infected group members (Loehle, 1995) and therefore the reduced social resting might be an avoidance behaviour of healthy individuals. On the other hand, due to agonistic behaviours towards sick individuals during this study, some of them were temporarily separated from the rest of the group to allow access to food and water. This might have influenced the frequency of social resting; however, it was also observed that individuals were resting in close proximity to each other on both sides of the separating barrier. Another possible explanation for the decrease in social resting could be the sampling protocol since only the frequency of resting occurrences was collected and not the duration of each instance. The animals could therefore have had a lower frequency of resting but with a longer duration. In contrast, social resting increased during Phase 3 after the animals were infected with FMDV. The increase in resting behaviour could be an evolutionary mechanism of energy conservation to facilitate a fever response. The apparent contradiction of less social resting when goats were sick with respiratory disease or infectious keratoconjunctivitis compared to the increases observed during Phase 3 could be due to the type of disease. For example, FMDV infected individuals did not show obvious signs of sickness behaviour, such as a hunched position, as the goats affected with infectious keratoconjunctivitis and respiratory disease often did. Therefore, FMD affected individuals might not have been identified by herd members as sick individuals that need to be avoided. Another explanation would be the number of affected animals. Non-FMD sicknesses only affected a few individuals in each group, while nearly all individuals (35/37) were infected with FMDV. Therefore, it was not possible to avoid contact with other FMDV infected animals in effort to avoid disease transmission.

Lameness is one of the first signs of FMDV infection in sheep (Kitching and Hughes, 2002). In our study, clinical lameness was not detected and there was no significant association between FMD induced foot lesions and the number of daily steps. However, the number of daily steps for two of the four individuals did descriptively reduce during the time when foot lesions were present. In cows, reduced walking activity due to lameness can be detected before the onset of clinical lesions (Mazrier et al., 2006). In contrast, in this study the reduction of steps due to foot lesions only started on the day the lesions were detected. A possible explanation for the lack of reduction of steps could be the small sample size of individuals that developed foot lesions. However, another explanation is that the foot lesions might not have been perceived as a disturbance by the affected goats. It has been suggested that FMD lesions occur at areas of increased friction (Nagendrakumar et al., 2015). The goats in this study were not required to walk far to access food and water, and therefore the limited walking required might have prevented the lesions from becoming severe and ultimately painful. Additionally, the flooring of the stables did not contain sharp obstacles like stones or uneven ground that could have exacerbated pressure points on the foot.

Although no difference in the step frequency was detected when animals showed FMD-related clinical signs, the number of steps taken decreased significantly when animals had fever. Fever plays a critical role in the recovery from an infection and therefore reduced activity is considered to be a strategy that helps to conserve energy in order to fully develop a fever response (Aubert, 1999; Hart, 1988).

During times of social instability, for example the regrouping of individuals, goats react with increased aggression towards each other (Andersen et al., 2008). At the beginning of this study, animals were randomly assigned into groups, partly with previously unknown individuals. Due to the new group settings, a new social hierarchy had to be established that might have increased aggressive behaviours including dominance gestures and displacements. During the course of the study agonistic and displacing behaviours decreased. A similar effect was reported in a study with feral goats in which aggressive behaviours after the introduction of unfamiliar individuals decreased after the first 24 hours (Alley and Fórdham, 1994). In this study, body weight was a significant predictor for the performance of agonistic behaviour with heavier individuals showing more agonistic and displacing behaviours compared to lighter individuals. This has also been reported in a study on angora goats (*Capra h. angoraensis*) in which aggressive attacks during feeding times were usually performed by heavier individuals towards lighter ones (Pretorius, 1970).

An animal's social environment has an impact on the motivation to engage in sickness behaviours depending on the costs and benefits of investing in such behaviours (Lopes, 2014). In mice, the position within the hierarchy has an influence on the expression of sickness behaviours. Subordinate individuals are more likely to suppress sickness behaviours in order to prioritise social behaviour in the presence of aggressive conspecifics, while dominant individuals express sickness behaviours (Cohn and de Sá-Rocha, 2006). The higher rank allows the dominant individuals to allocate resources into recovery, while subordinate individuals still need to display submissive behaviours (Cohn and de Sá-Rocha, 2006; Lopes, 2014). Agonistic behaviour decreased significantly when individuals were showing signs of a non-FMD sickness, possibly due to the expression of sickness behaviours of dominant individuals. Individual goats within this study were not able to defend their dominance status throughout non-FMD sicknesses and decreased in their rank, suggesting that other individuals took advantage of their weakness. Similarly, in wild Toque macaques injured individuals not only started less aggressive encounters during the recovery phase, but also often received more aggression and lost dominance rank (Dittus and Ratnayeke, 1989). In this study, the infection with FMDV did not influence the dominance rank of individual goats, and therefore this is not an adequate behavioural marker for an early detection of FMDV infections in goats.

Although displacing behaviour decreased over the time of the study period, being displaced did not change and yielding even increased, suggesting that the same individuals were still being displaced, but these agonistic behaviours were initiated by fewer individuals.

The detection of behavioural changes due to a health challenge can depend on the severity of infection and the pathophysiological consequences within the individual (Szyszka and Kyriazakis, 2013). This study is part of a larger project concerning FMD vaccine efficacy and the vaccination might have reduced the FMD-induced behavioural changes especially in animals receiving the higher doses of the vaccine. In cattle, it has been suggested that a threshold dose of pathogens is required before behavioural changes secondary to a parasitic infestation can be detected (Szyszka and Kyriazakis, 2013). A potential limitation of the current study is that all behaviours were summarised by phase, creating one data point per individual per phase, thus reducing the statistical power to detect differences. Further studies on a larger sample size of unvaccinated, as well as naturally infected goats will provide a better understanding of the behavioural changes associated with FMDV infections in goats. Furthermore, the presented data might be SAT1 specific and not generalisable to infections with all FMDV serotypes as other FMDV strains could be more virulent in goats. A further limitation of the study design, as due to logistical challenges during the trial, formal randomisation and the maintenance of a strict observation schedule was not possible. The observation length also varied between phases in effort to observe all animals every day post FMDV challenge. The study was designed in conjunction with the evaluation of the FMD vaccine to reduce the number of goats requiring FMDV infection and subsequently euthanasia; the current study was not exclusively designed to observe behavioural changes in the animals for ethical reasons. A random effect term was added to statistical models to adjust for vaccine dose and other potential group effects. However, the daily handling of goats and repeated specimen collections as part of the vaccine evaluation had an unknown effect on behavioural responses; inferences from the current study should be tempered by this potential source of bias.

5. Conclusions

The goats in this study showed signs of FMD and non-FMD related sicknesses. During the occurrence of non-FMD sicknesses, goats expressed sickness behaviours including a hunched posture and reduced social interactions. However, when affected with FMD, the animals did not have a reduction in feeding, as is commonly believed to occur. This suggests that the study goats did not perceive the oral lesions as a disturbance. Similarly, clinical lameness was not apparent and daily activity (number of steps) did not consistently decrease in the presence of FMD foot lesions. Therefore, individual goats infected with FMDV might be undetected within a flock due to the absence of obvious sickness behaviours including anorexia, depression and lameness. Our findings emphasise the importance of thorough examinations of all goats within flocks since animals with clinical lesions could not readily be differentiated from unaffected herd mates. This can have implications as infection could be spread between herds due to animal movements or inter-flock contacts within FMD affected rural communities.

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Table 1. Mean (range) percentage of time that each animal spent performing daily activities during a foot-and-mouth disease SAT1 experimental infection study of indigenous South African goats using 5-minute scan sampling.

Variable		Stable 1 (n=10)	Stable 2 (n=9)	Stable 3 (n=5)	Stable 4 (n=5)	Stable 5 (n=8)
Walking						
%	P1	6 (1 – 11)	8 (1 – 14)	11 (2 – 17)	4 (0 – 7)	9 (3 – 19)
	P2	8 (4 – 11)	6 (0 – 12)	5 (0 – 8)	8 (5 – 10)	8 (4 – 13)
	P3	7 (0 – 13)	5 (0 – 12)	5 (0 – 12)	8 (3 – 13)	8 (3 – 18)
Resting						
Total %	P1	56 (43 – 88)	54 (31 – 75)	45 (23 – 72)	49 (32 – 75)	47 (13 – 74)
	P2	53 (26 – 65)	60 (48 – 80)	52 (45 – 58)	37 (27 – 48)	51 (38 – 72)
	P3	43 (28 – 65)	64 (47 – 72)	50 (42 – 67)	38 (13 – 67)	51 (43 – 63)
Standing	P1	22 (8 – 67)	18 (2 – 52)	15 (8 – 19)	17 (6 – 43)	33 (3 – 95)
	P2	23 (4 – 56)	18 (8 – 38)	11 (3 – 23)	15 (5 – 28)	16 (6 – 26)
	P3	18 (2 – 48)	22 (8 – 48)	17 (12 – 23)	22 (7 – 42)	17 (3 – 42)
Laying	P1	34 (21 – 47)	37 (23 – 67)	29 (16 – 54)	32 (25 – 37)	20 (0 – 50)
	P2	30 (10 – 47)	41 (17 – 70)	41 (27 – 52)	22 (20 – 28)	34 (14 – 60)
	P3	24 (5 – 45)	41 (23 – 63)	33 (25 – 43)	16 (2 – 27)	33 (17 – 53)
Feeding						
%	P1	24 (8 – 35)	24 (14 – 35)	17 (2 – 25)	20 (10 – 32)	27 (8 – 57)
	P2	27 (13 – 50)	24 (3 – 45)	15 (5 – 23)	30 (18 – 40)	24 (13 – 40)
	P3	36 (23 – 52)	23 (13 – 37)	18 (12 – 25)	22 (10 – 38)	20 (3 – 43)

P1: Time between first and second FMD vaccination (20 d). P2: Time between second vaccination and until FMDV experimental challenge (21 d). P3: post-challenge (14 d).

Table 2. Multivariable model outputs for daily activities during a foot-and-mouth disease SAT1 experimental infection study of indigenous South African goats. Significant results are indicated in bold.

Variable		Estimate (95% CI)	Std error	t value	p value
Walking					
	P1	Reference			
	P2	-0.568 (-2.347, 1.212)	0.909	-0.625	0.534
	P3	-0.757 (-2.536, 1.022)	0.909	-0.833	**0.407**
Resting					
	P1	Reference			
	P2	2.270 (-2.769, 7.310)	2.573	0.882	0.380
	P3	-0.081 (-5.121, 4.958)	2.573	-0.032	0.975
Sex					
	Female	Reference			
	Male	-8.032 (-13.661, -2.561)	2.787	-2.881	**0.007**
Feeding					
	P1	Reference			
	P2	0.081 (-4.129, 4.291)	2.149	0.038	0.970
	P3	0.595 (-3.616, 4.805)	2.149	0.277	0.783

CI: Confidence interval. P1: Time between first and second FMD vaccination (20 d). P2: Time between second vaccination and until FMDV experimental challenge (21 d). P3: post-challenge (14 d).

Table 3. Mean (range) rate (count per hour) that each animal spent performing social activities during a foot-and-mouth disease SAT1 experimental infection study of indigenous South African goats using continuous sampling

Variable		**Stable 1 (n=10)**	**Stable 2 (n=9)**	**Stable 3 (n=5)**	**Stable 4 (n=5)**	**Stable 5 (n=8)**
Social feeding						
Count/hr	P1	2 (1 – 3)	2 (0 – 5)	2 (0 – 4)	1 (0 – 2)	1 (0 – 3)
	P2	2 (0 – 5)	2 (1 – 5)	2 (0 – 2)	2 (1 – 3)	1 (0 – 2)
	P3	3 (2 – 4)	4 (2 – 6)	2 (0 – 3)	1 (0 – 1)	1 (0 – 2)
Social resting						
Count/hr	P1	4 (0 – 8)	2 (0 – 4)	4 (4 – 5)	3 (2 – 3)	2 (0 – 3)
	P2	5 (0 – 7)	3 (2 – 4)	4 (3 – 4)	2 (1 – 3)	2 (0 – 6)
	P3	3 (1 – 4)	6 (4 – 8)	3 (0 – 5)	2 (0 – 3)	4 (1 – 8)
Agonistic behaviours						
Count/hr	P1	2 (0 – 5)	1 (0 – 2)	2 (0 – 7)	1 (0 – 3)	2 (0 – 7)
	P2	2 (0 – 5)	1 (0 – 4)	1 (0 – 3)	3 (0 – 9)	2 (0 – 11)
	P3	3 (0 – 6)	1 (0 – 2)	1 (0 – 3)	1 (0 – 3)	2 (0 – 7)
Displaced						
Count/hr	P1	0 (0 – 1)	0 (0 – 1)	0 (0 – 1)	0 (0 – 1)	0 (0 – 2)
	P2	0 (0 – 1)	0 (0 – 1)	0 (0 – 0)	0 (0 – 1)	0 (0 – 0)
	P3	0 (0 – 2)	0 (0 – 0)	0 (0 – 0)	0 (0 – 1)	0 (0 – 0)
Displacing						
Count/hr	P1	0 (0 – 1)	0 (0 – 1)	0 (0 – 1)	0 (0 – 1)	0 (0 – 2)
	P2	0 (0 – 1)	0 (0 – 1)	0 (0 – 0)	0 (0 – 1)	0 (0 – 1)
	P3	0 (0 – 1)	0 (0 – 0)	0 (0 – 0)	0 (0 – 1)	0 (0 – 0)
Yield						
Count/hr	P1	1 (0 – 5)	1 (0 – 3)	2 (0 – 5)	1 (0 – 2)	2 (0 – 6)
	P2	2 (0 – 4)	1 (0 – 3)	1 (0 – 2)	3 (0 – 6)	1 (0 – 5)
	P3	3 (0 – 7)	1 (0 – 5)	1 (0 – 3)	1 (0 – 3)	2 (0 – 5)

P1: Time between first and second FMD vaccination (20 d). P2: Time between second vaccination and until FMDV experimental challenge (21 d). P3: post-challenge (14 d).

Table 4. Multivariable model outputs for social behaviours during a foot-and-mouth disease SAT1 experimental infection study of indigenous South African goats. Rates were transformed using the natural logarithm prior to analysis and significant results are indicated in bold.

Variable		Estimate (95% CI)	Std error	t value	p value
Social feeding					
	P1	Reference			
	P2	-0.006 (-0.317, 0.307)	0.160	-0.034	0.973
	P3	0.379 (0.055, 0.702)	0.166	2.282	**0.025**
Non-FMD disease*					
	No	Reference			
	Yes	-0.466 (-0.882, -0.042)	0.216	-2.161	**0.033**
Social resting					
	P1	Reference			
	P2	-0.063 (-0.281, 0.155)	0.112	-0.563	0.575
	P3	0.478 (0.245, 0.711)	0.120	3.973	**<0.001**
Weight (kg)		0.025 (0.005, 0.044)	0.010	2.428	**0.019**
Non-FMD disease*					
	No	Reference			
	Yes	-0.465 (-0.751, -0.178)	0.148	-3.135	**0.002**

CI: Confidence interval. P1: Time between first and second FMD vaccination (20 d). P2: from second vaccination until FMDV experimental challenge (21 d). P3: post-challenge (14 d). * non-FMD diseases are infectious keratoconjunctivitis and respiratory disease.

Table 5. Multivariable model outputs for dominance behaviours during a foot-and-mouth disease SAT1 experimental infection study of indigenous South African goats. Data were rank transformed prior to statistical analysis and significant results are indicated in bold.

Variable		**Estimate (95% CI)**	**Std error**	**t value**	**p value**
Agonistic behaviours					
	P1	Reference			
	P2	-13.475 (-22.691, -4.199)	4.771	-2.824	**0.006**
	P3	-6.837 (-17.469, 3.835)	5.499	-1.243	0.217
Weight (kg)		3.587 (2.255, 4.938)	0.689	5.206	**<0.001**
Respiratory disease					
	No	Reference			
	Yes	-16.592 (-29.305, -3.800)	6.579	-2.522	**0.013**
Displacing					
	P1	Reference			
	P2	-16.924 (-28.192, -5.588)	5.797	-2.919	**0.004**
	P3	-19.046 (-31.335, -6.689)	6.333	-3.007	**0.003**
Weight (kg)		2.120 (0.673, 3.587)	0.745	2.844	**0.006**
Displaced					
	P1	Reference			
	P2	-3.811 (-13.960, 6.338)	5.182	-0.735	0.464
	P3	-5.351 (-15.500, 4.798)	5.182	-1.033	0.305
Yield					
	P1	Reference			
	P2	-0.265 (-7.545, 7.022)	3.759	-0.071	0.944
	P3	8.838 (1.152, 16.542)	3.972	2.225	**0.029**
Sex					
	Female	Reference			
	Male	-26.471 (-43.628, -9.302)	8.930	-2.964	**0.005**
Non-FMD disease*					
	No	Reference			
	Yes	-22.438 (-34.776, -10.008)	6.396	-3.508	**<0.001**

CI: Confidence interval. P1: Time between first and second FMD vaccination (20 d). P2: Time between second vaccination and until FMDV experimental challenge (21 d). P3: post-challenge (14 d). *non-FMD diseases are infectious keratoconjunctivitis and respiratory disease.

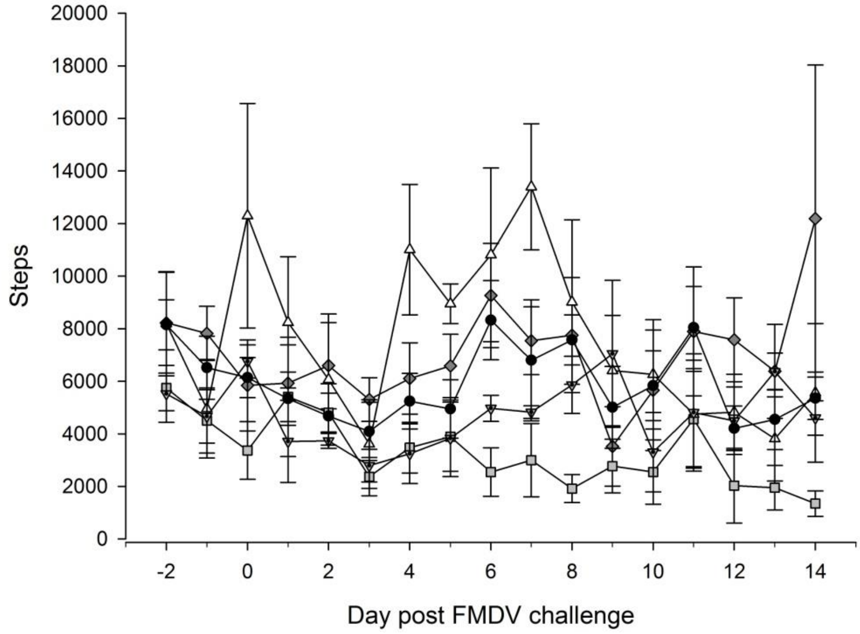

Figure 1. Average steps taken per treatment group (stable) during a foot-and-mouth disease SAT1 experimental infection study of indigenous South African goats. Each line / symbol represents a different stable and error bars correspond to the standard error of the mean. Day 0 is the day of experimental challenge.

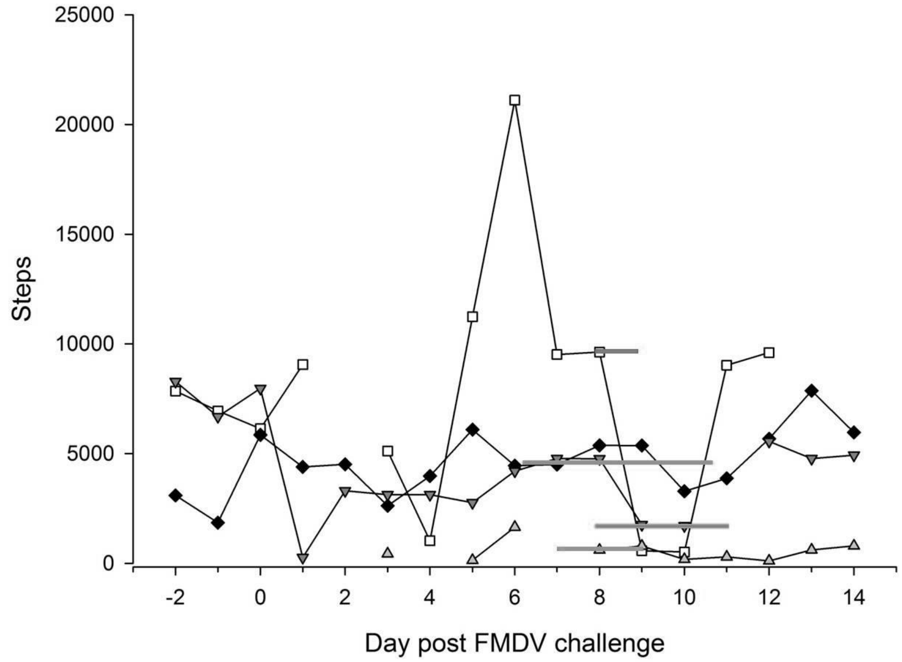

Figure 2. Steps taken by the four individuals with FMD foot lesions during a foot-and-mouth disease SAT1 experimental infection study of indigenous South African goats. Day 0 corresponds to the day of experimental challenge. Duration of lesions are marked: Individual 1 (square): day 8 to 9, Individual 2 (diamond): day 6 to 11, Individual 3 (down triangle): day 6 to 11, Individual 4 (triangle up): day 7 to 9.